AN INTEGRATIVE ASSESSMENT OF THE EFFECTS OF TAMARISK ON STOPOVER ECOLOGY OF A LONG-DISTANCE MIGRANT ALONG THE SAN PEDRO RIVER, ARIZONA

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ABSTRACT.—The riparian habitats of the arid southwestern United States provide critical stopover habitat for avian migrants, but they have been severely altered by invasive tamarisk (*Tamarix* spp.). The responses of birds to such habitat alterations are not well understood. We combined ecological and physiological measurements to provide an integrative assessment of how tamarisk invasion affects the stopover ecology of vernally migrating Wilson's Warblers (*Wilsonia pusilla*) along the San Pedro River in Arizona. Despite higher arthropod biomass in native cottonwood–willow habitat, the refueling rate of Wilson's Warblers, as measured by plasma metabolite profiling, was higher in tamarisk. Density and detections of Wilson's Warblers did not differ between habitats, but both measurements were significantly higher in cottonwood–willow habitat for the other members of the Wilson's Warbler foraging guild. Our measurements of food resources and migrant densities suggest that cottonwood–willow may provide high-quality stopover habitat. But when plasma metabolites are included, our results indicate that tamarisk offers superior habitat for refueling Wilson's Warblers, possibly because of release from high interspecific competition in cottonwood–willow. Our results demonstrate the importance of measuring refueling performance in the assessment of stopover habitat quality and the value of including plasma metabolite profiling in studies of avian stopover ecology. *Received 7 August 2009, accepted 3 January 2010.*

Key words: competition, fat, migrant songbirds, migration, physiological ecology, plasma metabolites, stopover sites, tamarisk, *Wilsonia pusilla*, Wilson's Warbler.

Una Evaluación Integral de los Efectos del Tamarisco sobre la Ecología de las Paradas Migratorias de un Migrante de Distancias Largas a lo largo del Río San Pedro, Arizona

RESUMEN.—Los ambientes ribereños del sudoeste árido de los Estados Unidos brindan ambientes de parada migratoria críticos para las aves migrantes, pero han sido alterados severamente por el tamarisco invasor (*Tamarix* spp.). Las respuestas de las aves a dichas alteraciones del hábitat no son bien conocidas. Combinamos medidas ecológicas y fisiológicas para proveer una evaluación integral de cómo la invasión del tamarisco afecta la ecología de las paradas migratorias de individuos migrantes vernales de la especie *Wilsonia pusilla* a lo largo del río San Pedro en Arizona. A pesar de que existe una mayor biomasa de artrópodos en ambientes de *Populus* y *Salix*, la tasa de reabastecimiento de las aves, medida mediante perfiles de metabolitos del plasma, fue mayor en los ambientes de tamarisco. La densidad y las detecciones de *W. pusilla* no difirieron entre hábitats, pero ambas medidas fueron significativamente mayores en ambientes de *Populus–Salix* para los otros miembros del gremio de forrajeo de *W. pusilla.* Nuestras medidas de los recursos alimenticios y las densidades de migrantes sugieren que los ambientes de *Populus–Salix* pueden ser hábitats de alta calidad para las paradas migratorias. Sin embargo, cuando los metabolitos plasmáticos son considerados, nuestros resultados indican que el tamarisco brinda un hábitat superior para los individuos de *W. pusilla* que se están reabasteciendo, posiblemente debido a una reducción de la fuerte competencia interespecífica que ocurre en los ambientes de *Populus–Salix.* Nuestros resultados demuestran la importancia de medir el desempeño en el reabastecimiento para evaluar la calidad de los ambientes de paradas migratorias y el valor de incluir los perfiles de metabolitos plasmáticos en estudios sobre la ecología de las paradas de las aves migratorias.

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Events During Migration have profound effects on the life cycle of avian migrants (Moore et al. 1995, Hutto 1998). Survivorship may be greatly reduced during migratory periods (Sillett and Holmes 2002), and reproductive success can be adversely affected either by late arrival to the breeding grounds (Cristol 1995) or because migrants carry inadequate energy stores to support breeding upon arrival (see Sandberg and Moore 1996). The challenge of migration is compounded by the fact that most migrants cannot deposit enough fuel to complete migration in a single nonstop flight and must stop periodically to replenish energy stores. The rate of refueling during stopover will directly influence the speed and success of migration and is an indicator of stopover habitat quality (Alerstam and Hedenström 1998, Weber et al. 1998). Thus, the availability of stopover habitats that provide sufficient resources for rapid refueling is critical for the overall success of migration and the fitness of migratory birds.

In the arid zones of the southwestern United States, vernal migrants overwhelmingly prefer riparian areas to the surrounding uplands for stopover habitat (see Carlisle et al. 2009). However, riparian areas account for <1% of the landscape in the Southwest and have been severely degraded by human use and the invasion of exotic vegetation (Ohmart 1994). Tamarisk (*Tamarix* spp.) is considered the most widespread of these invasive plant species (e.g., Howe and Knopf 1991, Lovich and de Gouvenain 1998). The continued and widespread alteration and loss of native riparian vegetation has led to considerable interest in how avian migrants respond to tamarisk invasion of critical stopover habitat.

Conclusions from studies of breeding and migrating birds along several southwestern drainages have been mixed, possibly because of drainage-specific conditions and vegetation structure (for a more complete discussion, see Walker 2006). Some reported that tamarisk supports lower densities and less diverse assemblages of birds (e.g., Anderson et al. 1977, Hunter et al. 1988). Some suggested that tamarisk can support equal or higher bird densities, total abundance, and species richness compared with native vegetation (e.g., Hunter et al. 1985, Walker 2008), and others considered tamarisk to be suitable habitat for some migrants (Ellis 1995, Yong and Finch 2002). In a recent analysis of avian communities, van Riper et al. (2008) concluded that an intermediate level of tamarisk invasion provides optimal habitat for migratory bird communities.

The dependence of these research findings and subsequent management recommendations on bird distribution data (i.e., abundance and diversity measurements; e.g., Ellis 1995, van Riper et al. 2008, Walker 2008) is striking. However, the abundance or presence of migrants at a particular stopover site does not necessarily correlate with performance or stopover-site quality. For example, the topography can cause large numbers of migrants to congregate at stopover sites, which results in mass loss during stopover (Hansson and Pettersson 1989), and refueling rates can be negatively affected by migrant density (Moore and Yong 1991, Kelly et al. 2002). Furthermore, migrants may not be able to assess the quality of available habitats immediately upon arrival (e.g., Paxton et al. 2008). Extensive exploration of available habitats may be costly (e.g., increased predation risk; Cimprich et al. 2005), and many migrants stop only briefly in unfamiliar territory. For example, average stopover lengths for Wilson's Warblers (*Wilsonia pusilla*; hereafter "warblers") during spring migration at different riparian areas in southern Arizona are <1 day (Hays 2008),

<5 days (Paxton et al. 2008), and estimated at <2 days (McGrath et al. 2009). Under these circumstances, migrants may be unable to effectively track resources during stopover, which can result in overuse of marginal habitats and a reduction in refueling performance (Shochat et al. 2002). Moreover, evidence that birds preferentially select exotic-dominated habitat that negatively affects performance (Remeš 2003, Lloyd and Martin 2005) urges caution when interpreting avian responses from studies that lack performance measurements, yet few comparisons of avian stopover ecology between tamarisk and native habitats include measurements of refueling performance (but see Yong et al. 1998).

Plasma metabolite profiling, a physiological technique used to assess refueling performance, has gained repute in recent studies of stopover ecology because it provides a measurement of performance from small numbers of single captures (Guglielmo et al. 2005). Thus, metabolite profiling avoids some of the potential capture biases and the large sampling efforts associated with other methods that are commonly used to estimate refueling performance, such as recapture analysis (e.g., Moore and Kerlinger 1987) and mass versus time-of-day regression (e.g., Carlisle et al. 2005; for a more complete discussion, see Jenni and Schwilch 2001, Guglielmo et al. 2005). The underlying concept of metabolite profiling is that circulating metabolites related to fat metabolism reflect metabolic state (i.e., feeding or fasting). Plasma triacylglycerol (TRIG), the major storage and transport form of dietary and hepatic-synthesized lipids, increases during feeding and fat deposition, whereas plasma glycerol (GLYC) and beta-hydroxybutyrate (BUTY) increase during fasting and exercise as a result of mobilization and oxidation of lipid stores (Robinson and Williamson 1980, Ramenofsky 1990). Plasma phospholipids (PL) offer additional information on refueling performance by signifying an additional pathway for dietary fatty acid transport and by providing insight into diet quality (Guglielmo et al. 2002b, 2005; Cerasale and Guglielmo 2006b).

Plasma metabolite profiles are predictive of body-mass changes in several species under captive conditions (e.g., Jenni-Eiermann and Jenni 1994, Williams et al. 1999, Cerasale and Guglielmo 2006a). Metabolites change within minutes in response to alteration of feeding rate (Zajac et al. 2006) and have been validated under field conditions. Metabolites reflect changes in body mass in recaptured migrants (Anteau and Afton 2008) and refueling performance at stopover sites of known low or high quality (Guglielmo et al. 2005). Metabolite analysis has been used in numerous studies to provide insight into the biology of avian migration (e.g., Guglielmo et al. 2002a, Ydenberg et al. 2002, Seaman et al. 2006). Here, we combine plasma metabolite profiling with measurements of ecological variables to provide an integrative assessment of how tamarisk invasion influences the stopover ecology of vernally migrating warblers along the San Pedro River in Arizona. Our expectation is that if tamarisk is inferior stopover habitat for migrating warblers in comparison with native cottonwood–willow, then refueling rates will be lower in habitat dominated by invasive tamarisk.

Methods

Study area.—The study area consisted of six sites established along the upper San Pedro River in the San Pedro Riparian National Conservation Area, Arizona (Fig. 1). Cottonwood–willow sites were dominated (55–75%; Stromberg et al. 2006) by Fremont
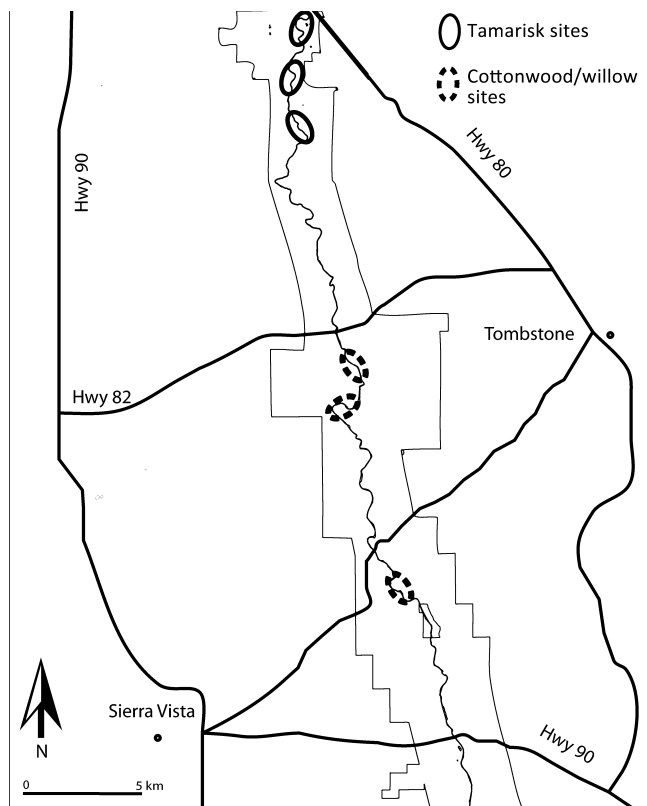
FIG. 1. Map of the study area along the upper San Pedro River in the San Pedro Riparian National Conservation Area, Arizona.

Cottonwood (*Populus fremontii*) and Goodding's Willow (*Salix gooddingii*) and contained modest amounts (12–35%; Stromberg et al. 2006) of mesquite (*Prosopis* spp.) and a few tamarisk shrubs. Tamarisk sites were located in ephemeral reaches dominated by tamarisk vegetation (70–80%; Stromberg et al. 2006, L. A. Brand et al. unpubl. data) and contained ~10% cottonwood–willow vegetation and ~10% mesquite (Stromberg et al. 2006). Habitats with similar levels of tamarisk invasion are considered tamarisk habitat in other riparian ecosystems in Arizona, and avian migrants respond equivalently to these habitats and pure tamarisk stands (van Riper et al. 2008). Thus, we hereafter refer to tamarisk-dominated sites as "tamarisk." All sites were located within the riparian corridor, and the surrounding uplands were dominated by mesquite woodlands. Sites were 12–16 ha in area and were separated by ≥800 m. Ideally, we would have liked to establish sites such that tamarisk sites were interspersed with cottonwood–willow sites. This was not possible along the section of the San Pedro where our study was conducted. However, it is likely that the distance between our tamarisk and cottonwood–willow sites was sufficiently small that migrants could choose between both habitats.

Measurement of refueling performance.—Warblers were captured in mist nets between 14 April and 25 May 2003. To ensure equal sampling of habitats throughout the season, two field crews were used to capture birds in both tamarisk and cottonwood–willow habitat each day and capture efforts were systematically rotated among sites. To accurately estimate the time between capture and blood sampling (bleedtime), nets were continuously monitored between 0600 and 1200 hours Mountain Standard Time (MST). Immediately after capture, we collected ~100 μL whole blood by brachial venipuncture. Plasma was separated, flash frozen in liquid nitrogen dry shippers (Taylor-Wharton Cx-100), and then stored at –80°C until analysis. Birds were then banded and weighed (±0.1 g), and fat score was visually quantified according to a six-point scale defined by Helms and Drury (1960), with 0 denoting "no observable fat" and 5 signifying "fat overflowing the furculum." We sexed and aged each bird when possible, following Pyle et al. (1987).

Before laboratory analyses, plasma was diluted three-fold with 0.9% NaCl. Metabolites were measured via colorimetric enzymatic endpoint assays in 400 μL flat-bottomed microplates using a microplate spectrophotometer (BioTek Powerwave X340). We measured TRIG and GLYC as described by Guglielmo et al. (2002a), and BUTY and PL as described by Guglielmo et al. (2005).

Food availability.—Arthropods on vegetation were sampled bimonthly at each site (7 April–21 May 2003). During each sampling session, 18 trees or shrubs at each site were chosen by random distances and compass bearings. A combination of sweep-net and beat-sheet techniques was used to collect both sessile and active foliage-dwelling arthropods that foragers such as warblers consume (Cooper and Whitmore 1990). Warblers are mainly insectivorous during migration and forage at an average foliage height between 1 and 2.5 m (see Ammon and Gilbert 1999). Thus, half of the chosen vegetation was sampled between 0.5 and 1.5 m and the remaining between 1.5 and 3 m. At each chosen plant, a foliage volume 1 m in depth, 2 m in length, and 1–1.5 m in height (see above) was swept 10 times and beat 10 times above a 1-m² sheet. Arthropods were collected with aspirators, killed by freezing, grouped into size classes by length (0–5 mm, 5–10 mm, 10–15 mm, 15–20 mm, 20–25 mm, 25–30 mm, <30 mm), dried at 60°C for 72 h, and weighed by group on a digital balance (±0.001 g). Biomass of arthropods <10 mm in length (hereafter "biomass") was used for analyses because larger arthropods are consumed infrequently by warblers (Raley and Anderson 1990).

Quantification of foraging behavior can be superior to measurement of overall food abundance alone as a means of describing food availability (Hutto 1990). We recorded attack rate as a measurement of food availability. Attack rate is positively related to prey availability in several species (Robinson and Holmes 1984, Hutto 1990, Lovette and Holmes 1995). Warblers were followed at each site, and direct observations of foraging behavior were dictated into a minicassette recorder. The number of foraging attempts per minute was subsequently calculated during playback using a digital timer. Observations in which foraging behavior could not be clearly seen were excluded from calculations, and only observations lasting >20 s were used for analysis.

Diet quality.—Total body TRIG:PL is used as a measure of condition in invertebrates because PL reflects overall body size and TRIG indicates the amount of lipid storage (Hill et al. 1992, Hentschel 1998). We measured plasma TRIG:PL in warblers' plasma because it may, in turn, reflect invertebrate TRIG:PL and be an indicator of diet quality (Cerasale and Guglielmo 2006b).

Migrant counts and densities.—To compare the number of warblers and their potential avian food competitors between habitats, counts of migrants were made in each habitat type during

seven weekly point counts (7 April–21 May 2003). Five points separated by ≥100 m were established at each site. Each week at every point, we recorded the number of individuals of each species seen and heard within a 50-m radius during a 5-min count (Dettmers et al. 1999). All counts were conducted between 0600 hours (sunrise) and 1130 hours MST. All but counts at two sites during the first sampling session were performed by a single observer to reduce observer variability. The visitation order of points and sites was rotated systematically to limit bias from time of day on comparisons of detections between habitat types. Species were considered potential food competitors of warblers (hereafter "competitors") on the basis of diet and foraging microhabitat as described by Skagen (1995). See Brand et al. (2009) for a complete list of species detected.

Statistical analyses.—All analyses were performed using SAS, version 9.0 (SAS Institute, Cary, North Carolina). Linear mixed models were used to test for differences in metabolites, counts of migrants, arthropod biomass, and foraging attack rate between habitat types. Sites were considered random samples of habitats and included as a random factor nested within habitat in all linear mixed models. Differences between habitats were considered significant at $P < 0.05$ in all models except when Bonferroni corrections were made.

We used one-way analysis of variance to test for differences in mass, fat score, and the proportion of female and second-year warblers captured between habitats. Body mass was regressed on the time of capture in an attempt to estimate refueling rates (e.g., Carlisle et al. 2005). Metabolite concentrations were ($\log_{10} + 1$) transformed to satisfy assumptions of normality. To test for differences in metabolites between habitats, body mass, bleedtime, Julian date and time of capture were entered as covariates, and habitat was entered as a categorical variable into mixed models with a compound symmetric (CS) covariance matrix. Covariates were retained in models at $P < 0.10$. In addition, we used principal component analysis (PCA) to test for differences in metabolites between habitats in multivariate space. The correlation matrix of metabolites was used in the PCA, and the differences between habitats in the resulting principal component scores were tested with multivariate analysis of variance. To test for a difference in plasma TRIG:PL between habitats, PL was included as a covariate explaining TRIG in a linear mixed model with a CS covariance matrix.

To account for repeated measures at the same site that were temporally correlated, an autoregressive order 1 (AR1) covariance matrix was used in mixed models that tested for differences in arthropod biomass between habitats. We included sampling session (as a continuous variable), habitat type, and their interaction in a model to test for a difference in arthropod biomass between habitats. An identical model, except for the inclusion of sampling session as a categorical variable, was used to generate linear contrasts to test for differences in biomass between habitats at a given sampling session. Bonferroni correction was again used to control for multiple comparisons. Foraging attack rate was ($\log_{10} + 1$) transformed to satisfy assumptions of normality. Julian date, habitat, and their interaction were included in linear mixed models with a CS covariance matrix to test for differences in foraging rates between habitats.

Two approaches were used to analyze potential competition from conspecifics and competitors of warblers. First, all detections of competitors throughout the migration season were combined, and DISTANCE (Thomas et al. 2010) was used to calculate detection probability and density measures. Separate detection functions were calculated for each habitat. In addition, the density of warblers and of Yellow Warblers (*Dendroica petechia*), the most abundant member of the warbler foraging guild along the San Pedro River (Skagen 1995), were each modeled separately. Because sample sizes of both species were small within each habitat, densities were calculated using detection functions with all detections of each species. Data from each avian group were bootstrapped 999 times to provide point and error estimates of densities. Using habitat-specific detection functions calculated from the detections of competitors to estimate the densities of warblers and Yellow Warblers did not improve density estimates or standard errors. Second, during each sampling session, the counts of competitors and warblers at points within each site were combined to yield the number of counts at each site. Across the migration season, this design yielded seven temporally correlated replicates of the mean number of counts for each site. Mean counts were square-root transformed to satisfy assumptions of normality. Sampling session (as a continuous variable), habitat type, and their interaction were included in mixed models with an AR1 covariance matrix to test for differences between habitats in the number of counts. Identical models, except for the inclusion of sampling session as a categorical variable, were used to generate linear contrasts and test for differences in counts between habitats at a given sampling session. Bonferroni correction was used to control for multiple comparisons.

Results

Food abundance and availability.—Biomass of arthropods <10 mm in length accounted for 81% and 87% of total biomass collected in cottonwood–willow and tamarisk, respectively. Biomass increased in both habitats as the season progressed (Fig. 2) but
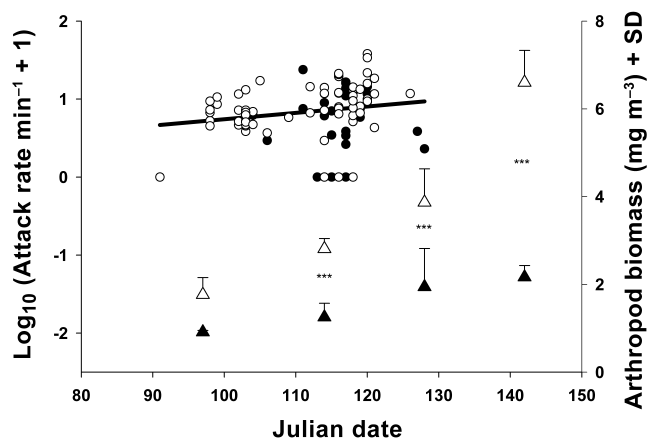

Fig. 2. Mean (+ SD) biomass (mg m^{-3}) of arthropods <10 mm in length per site for four bimonthly sampling sessions and attack rate per minute throughout the migratory season, 2003, along the San Pedro River in Arizona. The regression line represents the increase in attack rate as the season progressed and did not differ between habitats (see text). Closed and open circles (sampling session) and triangles (attack rates) are values for tamarisk and cottonwood–willow, respectively. Three asterisks (***) indicate significance after Bonferroni correction (see text).

Table 1. Functions used for modeling detection probability in the program DISTANCE (Thomas et al. 2010), detection probability, density, and number of detections used in analyses (*n*) for Wilson's Warblers (WIWA), Yellow Warblers (YRWA), and their potential food competitors (COMP) detected in cottonwood–willow (CW) and tamarisk (TAM) habitat along the San Pedro River in Arizona.

Habitat	Avian group	Key function + series expansion	Probability of detection	Density (birds ha^{-1})	*n*
CW	WIWA	Uniform + polynomial	0.49 (0.41–0.58)	20.22 (10.82–37.79)[a]	44
	YRWA	Uniform + cosine	0.34 (0.27–0.45)	47.00 (27.14–81.40)[a]	206
	COMP	Half-normal + cosine	0.26 (0.21–0.32)	131.36 (90.87–189.89)[a]	434
TAM	WIWA	Uniform + polynomial	0.49 (0.41–0.58)	11.02 (6.76–17.97)[a]	14
	YRWA	—	—	—	3
	COMP	Uniform + cosine	0.34 (0.31–0.37)	37.64 (27.59–50.36)[a]	162

[a]Log-normal 95% confidence intervals from bootstrap standard error estimates.
Note: No density estimates for YWAR are provided for tamarisk because of low sample size.

increased more rapidly in cottonwood–willow ($\beta_{\text{habitat*sampling session}}$ = 0.050, *F* = 25.00, df = 1 and 16, *P* < 0.001). Furthermore, with the exception of the first sample (*P* = 0.073), biomass was higher in cottonwood–willow during all sampling sessions (all *P* < 0.004; see Fig. 2).

We performed 71 foraging observations of warblers at cottonwood–willow sites and 31 at tamarisk sites. In agreement with results from arthropod sampling, attack rate increased as the migratory period progressed ($\beta_{\text{sampling session}}$ = 0.024, *F* = 7.87, df = 1 and 94, *P* = 0.006; Fig. 2), but this relationship did not differ between habitats (*P* > 0.58). Overall, attack rates did not differ between habitats (*P* > 0.53). Observer had no qualitative effect on our results.

Migrant counts and density.—For analyses using DISTANCE, we excluded detections beyond 44 m, 28 m, and 45 m for competitors, warblers, and Yellow Warblers, respectively, because the probability of detection was <0.1 (Buckland et al. 2001). For competitors, the detection function and detection probability differed between habitats (Table 1), and density was significantly higher in cottonwood–willow (confidence intervals did not overlap; Table 1). Density estimates for warblers were variable, likely because of low sample size, and did not differ significantly between habitats (confidence intervals overlapped; Table 1). The density of Yellow Warblers was high in cottonwood–willow but could not be estimated in tamarisk because of low sample size (Table 1).

Linear mixed models (see above) indicated that counts of warblers did not differ between habitats (*P* > 0.96) or during any sampling session after Bonferroni adjustment. However, during the third (*P* = 0.047), fifth (*P* = 0.017), and seventh (*P* = 0.057) sampling sessions, comparisons of the number of warblers in the two habitats exceeded or approached significance before Bonferroni adjustment (Fig. 3A). Counts of competitors increased as the season progressed, but the increase was less pronounced in cottonwood–willow than in tamarisk ($\beta_{\text{habitat*sampling session}}$ = −0.301, *F* = 8.04, df = 1 and 34, *P* < 0.008; Fig. 3B). However, counts of competitors were significantly higher in cottonwood–willow during five of the seven sampling periods (all *P* < 0.007), and mean counts were never higher in tamarisk (see Fig. 3B). Moreover, a large overall effect of habitat (*F* = 42.44, df = 1 and 4, *P* < 0.003) indicated that counts of competitors were higher in cottonwood–willow than in tamarisk.

Refueling performance and metabolites.—The number of captures of warblers varied between 16 and 30 among sites, and

totaled 50 and 77 in tamarisk and cottonwood–willow, respectively. The proportion of captures that were female tended to be higher at tamarisk sites (0.59 ± 0.10; mean ± SD) than at cottonwood–willow sites (0.42 ± 0.10), but the difference was not significant (*P* = 0.088). The proportion of second-year birds captured did
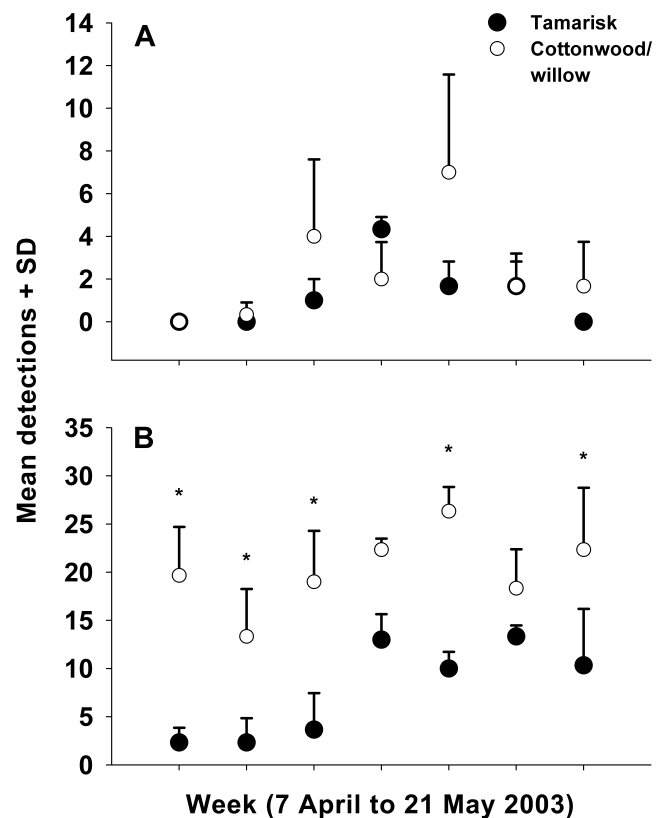

Fig. 3. Mean (+ SD) detections per site of (A) Wilson's Warblers and (B) all potential avian food competitors during seven weekly point counts throughout spring migration, 2003, along the San Pedro River in Arizona. Closed and open circles are values in tamarisk and cottonwood–willow sites, respectively. Potential competitors of Wilson's Warblers for food were chosen according to Skagen (1995). Asterisk (*) indicates significance after Bonferroni correction (see text).

Table 2. Relationships between covariates included in analyses and the plasma metabolites triacylglycerol (TRIG), glycerol (GLYC), B-OH butyrate (BUTY), and phospholipids (PL) in Wilson's Warblers captured along the San Pedro River in Arizona. 0 = no significant relationship ($P > 0.10$).

Covariate	Metabolite			
	TRIG	GLYC	BUTY	PL
Mass	Positive	Positive	Negative	Positive
Bleedtime	Negative	0	Positive	Negative
Time of day	0	0	0	Positive
Julian date	0	Negative	0	Positive

Table 3. Mean ± SD (mmol L^{-1}) concentrations of the plasma metabolites triacylglycerol (TRIG), glycerol (GLYC), B-OH butyrate (BUTY), and phospholipids (PL) in Wilson's Warblers captured in cottonwood–willow and tamarisk habitats along the San Pedro River in Arizona.

Habitat	Metabolite			
	TRIG	GLYC	BUTY	PL
Cottonwood–willow	2.58 ± 2.03	0.95 ± 0.50	1.23 ± 0.69	7.89 ± 1.59
Tamarisk	4.36 ± 3.86	1.15 ± 0.82	1.18 ± 0.76	8.45 ± 1.98

not differ between habitats ($P > 0.32$). Body mass was not related to the time of day at capture ($P > 0.14$), and neither fat score ($P > 0.69$) nor body mass ($P > 0.23$) differed between habitats. The effects of covariates on metabolites differed among metabolites (see Table 2).

Metabolite levels did not differ substantially among sites within a habitat type; variance for site nested within habitat was <2% of residual variance in all models. Plasma TRIG was significantly higher in warblers captured in tamarisk ($F = 16.33$, df = 1 and 4, $P < 0.016$; Fig. 4). Plasma BUTY, GLYC, and PL did not differ between habitats (all $P > 0.18$; Fig. 4; see Table 3 for descriptive statistics). Plasma TRIG was positively correlated with PL (Pearson's $r = 0.62$, $P < 0.0001$), and plasma TRIG:PL was significantly higher in warblers captured in tamarisk ($F = 12.78$, df = 1 and 4, $P = 0.023$; Fig. 4).

We excluded GLYC from the PCA of metabolites because its apparent dual signal in fat mobilization and deposition makes it difficult to interpret (see Guglielmo et al. 2005). Similar to our previous results (Guglielmo et al. 2005), TRIG and PL loaded
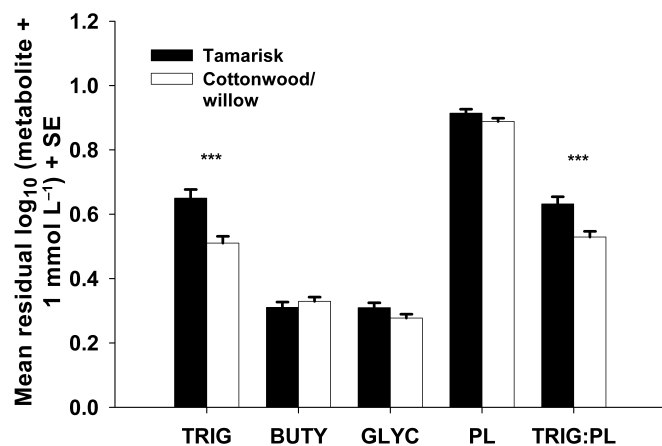
Table 4. Eigenvalue and eigenvector loadings from a principal component (PC) analysis of triacylglycerol (TRIG), B-OH butyrate (BUTY), and phospholipids (PL) in Wilson's Warblers captured along the San Pedro River in Arizona.

	Eigenvalue	Metabolite eigenvector loadings		
		TRIG	BUTY	PL
PC axis 1	1.75	0.68	−0.39	0.62
PC axis 2	0.91	0.09	0.88	0.46

positively and BUTY negatively onto the first principal component axis, whereas both BUTY and PL loaded positively onto the second principal component axis (Table 4 and Fig. 5). Thus, the first principal component axis represents a mass gain and loss axis, but the second axis is more difficult to interpret. The combination of both axes explained 89% of the variance in metabolites and signaled significantly higher refueling in tamarisk (Wilks's $\lambda = 0.93$, $F = 4.48$, df = 2 and 124, $P < 0.014$).

Fig. 4. Comparison of residual means (Log$_{10}$ metabolite + 1 mmol L^{-1} + SE) of plasma triacylglycerol (TRIG), glycerol (GLYC), beta-hydroxybutyrate (BUTY), phospholipids (PL), and triacylglycerol:phospholipid (TRIG:PL) from mixed model analyses (see text). Closed and open bars are values from Wilson's Warblers caught in tamarisk and cottonwood–willow, respectively, along the San Pedro River in Arizona. Three asterisks (***) indicate significance at $P < 0.05$.
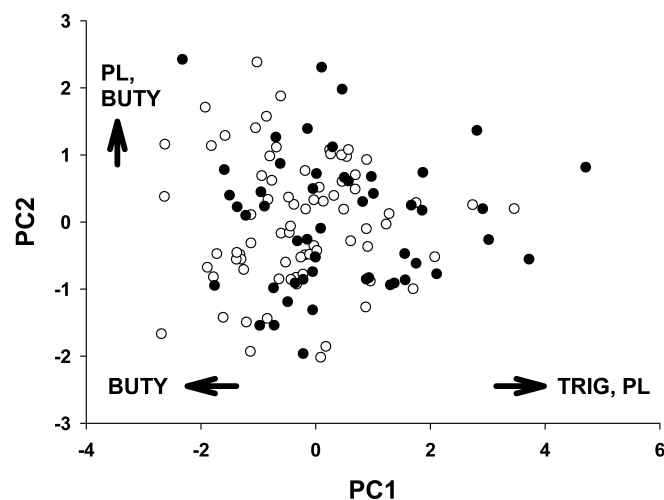

Fig. 5. First (PC1) vs. second (PC2) principal components from a principal component analysis of plasma triacylglycerol (TRIG), beta-hydroxybutyrate (BUTY), and phospholipids (PL) from Wilson's Warblers captured in cottonwood–willow (open circles) and tamarisk (closed circles) along the San Pedro River in Arizona.

DISCUSSION

Previous studies of avian responses to tamarisk invasion have based much of their findings on bird abundance and diversity measurements (e.g., Ellis 1995, van Riper et al. 2008). The underlying assumption of these studies is that stopover-site quality and avian performance are reflected in the number of migrants present during migratory stopover. This approach has been used to make management recommendations regarding the suitability of tamarisk habitat for avian migrants (e.g., van Riper et al. 2008, Walker 2008). However, several lines of evidence suggest that high avian abundance is not necessarily indicative of high refueling performance or stopover-site quality (e.g., Shochat et al. 2002, Ydenberg et al. 2002). Thus, measurement of migrant abundance and diversity alone is often insufficient to inform decisions regarding the management of stopover-habitat quality for migratory birds. In the present study, we combined traditional measures of stopover-habitat quality (migrant abundance and food availability) with plasma metabolite profiling, a physiological method used to estimate instantaneous rate of refueling. Our findings suggest that despite greater arthropod biomass in cottonwood–willow, warblers refueled more quickly in tamarisk, possibly as a consequence of release from high interspecific competition in cottonwood–willow habitat.

Food availability.—Although the risk of predation certainly influences migratory decisions and selection of stopover habitat (e.g., Moore et al. 1995, Ydenberg et al. 2002), the availability of food resources is regarded as the dominant influence on stopover ecology in the desert Southwest (McGrath et al. 2009). Tamarisk is generally considered to support lower arthropod abundance (e.g., DeLay et al. 1999, Yard et al. 2004, McGrath et al. 2009) than native vegetation, and a less diverse arthropod community (DeLoach et al. 2000, Wiesenborn 2005) with highly variable biomass (Wiesenborn 2005). Thus, tamarisk is thought to be of little benefit to Neotropical migrants, including Wilson's Warblers (DeLay et al. 1999, McGrath et al. 2009). However, along several southwestern drainages, including the San Pedro River (see Hannon et al. 2009), tamarisk can support higher arthropod abundances than native vegetation, although this increase is seen during the summer months after many en route migrants have departed.

Data from our study are in agreement with findings that suggest that tamarisk supports fewer insects for avian migrants than native habitats, because arthropod biomass was significantly higher in cottonwood–willow than in tamarisk. However, abundance of arthropods does not always coincide with food availability from an individual bird's perspective (see Hutto 1990), and quantification of avian foraging behavior has been used in combination with measurements of food abundance to provide a measure of food availability (Hutto 1990). We found no difference in attack rate between habitats, which suggests that the availability of arthropod prey did not differ between habitats.

Caution should be applied when interpreting results from observations of foraging behavior. We could not determine the success of individual foraging attacks, which can influence interpretations of attack rate. Additionally, foraging behavior may have been affected by the population dynamics of arthropod communities in adjacent habitats along the riparian corridor. We observed warblers at all sites foraging in mesquite vegetation that borders the riparian zone, particularly among exposed roots along the terrace that lines the river corridor (D. J. Cerasale unpubl. data), but comparisons of behavior between mesquite vegetation adjoining tamarisk and cottonwood–willow habitats were beyond the scope of the present study.

Diet quality.—The quality of consumed prey can affect fattening rates in avian migrants (e.g., Moore and Simm 1985, Bairlein 1998). For example, migrants may have to capture more low-quality individual prey to attain the energy intake from a few larger prey items. In invertebrate prey, total body TRIG is related to the amount of lipid stores, whereas PL is associated with structural membranes and is a function of body size (Hill et al. 1992, Hentschel 1998). Thus, invertebrate TRIG:PL indicates an individual's physiological condition and its nutritional quality to avian predators. In avian plasma, TRIG:PL is related to dietary TRIG:PL content (Cerasale and Guglielmo 2006b), which suggests that plasma TRIG:PL may provide information on diet quality.

Plasma TRIG:PL was higher in warblers caught in tamarisk, which suggests that higher refueling performance in tamarisk may be facilitated by the consumption of higher-quality invertebrate prey. Guglielmo et al. (2005) also found higher plasma TRIG:PL at a high-quality than at a low-quality stopover site. The ability to assess the quality of consumed food items has considerable value in studies of avian stopover ecology, and our results suggest that plasma TRIG:PL is a potential physiological tool for measuring avian diet quality and foraging costs. However, controlled studies coupled with information on landscape variability in prey TRIG:PL are needed before the utility of plasma TRIG:PL in field applications is fully known.

Potential competition.—The high energy requirements that birds face during migratory periods are often exacerbated by the potential for increased competition for food (Moore et al. 1995). High densities of migrants can depress food abundance during stopover (Moore and Yong 1991); thus, refueling rates may be negatively affected by the density of competitors at a stopover site (Kelly et al. 2002). In principle, higher numbers of migrants in cottonwood–willow might decrease arthropod abundance and reduce individual rates of refueling by warblers. Our data suggest that this was not the case; arthropod biomass did not decrease as the number of migrants increased. Alternatively, competition among migrants for access to available food resources can affect individual refueling rates (e.g., Carpenter et al. 1993), and numerous studies have documented aggression and territorial defense by migrants during stopover (e.g., Rappole and Warner 1976; Carpenter et al. 1983, 1993; Sealy 1988; Skagen 1995).

Neither counts nor overall density of warblers differed between habitats in our study. By contrast, density and counts of potential interspecific competitors were significantly and substantially higher in cottonwood–willow. These data complement previous reports from along the San Pedro River that showed that the abundance of warblers was negatively correlated with that of resident species in their foraging guild and with that of Yellow Warbler, the most abundant migrant and a common breeder that establishes territories during spring migration along the upper San Pedro River (Skagen 1995, Skagen et al. 1998). In fact, warblers were absent from sites with high densities of Yellow Warblers (Skagen 1995). We detected high numbers of Yellow Warblers in cottonwood–willow during the stopover period, but very few in tamarisk

(Table 1). Moreover, aggressive encounters between Yellow Warblers and warblers along the San Pedro River are known to occur (Skagen 1995, D. J. Cerasale pers. obs.), which suggests that interference competition could have been high in cottonwood–willow.

Refueling performance.—The mass-versus-time-of-day regression technique was not sensitive enough to detect differences in performance between habitats. This technique often requires a substantially larger sample size of captures to detect mass changes in migrants than was provided by our capture efforts (see Carlisle et al. 2005), although this is not always the case (see Guglielmo et al. 2005). However, plasma metabolite profiles indicated that warblers were refueling more rapidly in tamarisk.

Plasma triacylglycerol levels were significantly higher in warblers foraging in tamarisk, and principal component scores were indicative of higher fat deposition in tamarisk. Plasma triacylglycerol is likely the most informative of these metabolites for measuring refueling performance in the field because it changes rapidly in response to feeding rate (Zajac et al. 2006) and is predictive of mass changes in recaptured migrants (Anteau and Afton 2008) and at stopover sites of known quality (Guglielmo et al. 2005). Although TRIG can be affected by macronutrient composition and diet type (i.e., seed vs. fruit; Smith et al. 2007, Smith and McWilliams 2009), our previous work with captive passerines indicates that the relationship between TRIG and body-mass change is not affected by extreme changes in dietary lipid content (Cerasale and Guglielmo 2006a). Moreover, warblers foraging in tamarisk and cottonwood–willow were likely not eating foods that differed enough in nutrient composition to affect TRIG levels. Thus, the substantial difference in plasma TRIG indicated significantly higher fat deposition in tamarisk.

The difference in mean TRIG of warblers captured in tamarisk and cottonwood–willow along the San Pedro River (~1.5 mmol L^{-1}; see Table 2) is comparable to results for other migrating passerines in North America. A difference of 0.7–1.0 mmol L^{-1} in TRIG in Hermit Thrushes (*Catharus guttatus*) and Magnolia Warblers (*Dendroica magnolia*) that used two sites of different quality was associated with a difference of 0.5–1.0 g h^{-1} in refueling rate (Guglielmo et al. 2005). In captive warblers, TRIG concentration differed by ~4 mmol L^{-1} in birds that fed at rates equivalent to a loss of 0.22 g day^{-1} and a gain of 0.75 g day^{-1} (Zajac et al. 2006). However, under most circumstances, metabolites can provide only a relative measure of refueling performance, because species differences and the influence of environmental conditions preclude the calculation of exact refueling rates from single captures of migrants.

Plasma beta-hydroxybutyrate does not change as rapidly as TRIG in response to feeding regimes (Zajac et al. 2006) and may not be predictive of mass changes at high concentrations (Cerasale and Guglielmo 2006a). Thus, plasma BUTY may not have been sensitive enough to detect differences in metabolic state between habitats. Plasma glycerol also did not differ between habitat types, but GLYC is often an unsuitable metabolite for the prediction of body-mass changes because plasma concentrations can be high during both fat deposition and utilization (see Guglielmo et al. 2005). Plasma phospholipids may represent an additional pathway for the deposition of dietary fatty acids, and PL is often positively correlated with TRIG (Guglielmo et al. 2005). We found no difference in PL between cottonwood–willow and tamarisk, yet PL was positively correlated with TRIG and loaded positively with TRIG

onto the first principal component axis (Table 4), providing further evidence that PL may indicate fat deposition. However, the relationship between PL and body-mass changes is not consistent among species (Cerasale and Guglielmo 2006a), and further research is needed to evaluate the utility of incorporating plasma PL into metabolite profiles for assessment of refueling performance.

Conclusions.—Direct measurement of refueling rates allows for an integrative analysis of migratory stopover ecology and provides critical data for conservation and management efforts. Here, we have shown that plasma metabolites provide a powerful tool in ecological studies of migrant birds. Excluding the physiological data, our results suggest that cottonwood–willow may provide superior habitat for refueling warblers; prey biomass and the number of birds were significantly higher in cottonwood–willow. However, plasma metabolite information on refueling performance, coupled with the distribution and density of potential food competitors of warblers, suggests an alternative interpretation.

Plasma metabolite analysis clearly indicated that warblers refueled more quickly in tamarisk, possibly facilitated by higher-quality prey in that habitat. Moreover, we detected significantly more competitors of warblers in cottonwood–willow habitat. These data, combined with evidence that the abundance of this species decreases in the presence of competitors and that aggressive interactions between the two occur (Skagen 1995), suggest that warblers that use tamarisk may have better access to food resources. Thus, release from interspecific competition could allow warblers to attain higher refueling rates in tamarisk than are possible in cottonwood–willow. Increased interference competition does not necessarily lead to a detectable decrease in foraging rates (Vahl et al. 2005), which may help explain why we found no difference in our measure of foraging attack rate between habitats. Future studies that combine refueling performance, foraging behavior, and arthropod prey abundance may provide further evidence for this possibility.

Our results also extend our knowledge of avian response to tamarisk invasion to drainages other than those most commonly studied: the Colorado and Rio Grande rivers (e.g., van Riper et al. 2008, Walker 2008). Recent findings from the former imply that habitat selection and stopover ecology of warblers is driven mainly by the phenology of mesquite flowering (McGrath et al. 2009). However, leaf development in mesquite stands, which precedes flowering (Simpson 1977), does not begin along the upper San Pedro River until the middle of May (Scott et al. 2006, 2008). This date is after many migrants, including warblers, have already passed through the area (Skagen 1995, present study), which indicates that habitat selection and stopover ecology of warblers are likely influenced by different factors along the San Pedro River.

Evidence of higher refueling rates in tamarisk also complements findings that indicate that at least some migrants, including warblers, can tolerate tamarisk invasion (e.g., Walker 2008). However, although our results suggest that tamarisk may have value for some migrant passerines, we considered only one species of vernal migrant along a single southwestern drainage. Tamarisk may not provide suitable habitat for all migrant species (e.g., Anderson et al. 1977, Hunter et al. 1988, van Riper et al. 2008), including many competitors of warblers in the present study. Limited availability of native riparian vegetation may also necessitate the use of exotic habitats by migrants (Yong and Finch 2002), concentrate some

species in patches of native vegetation, and increase competition for resources. Restoration of native riparian habitats in the arid zones of the southwestern United States might improve refueling performance for many migrants, especially species that do not use monotypic tamarisk stands. However, complete eradication of tamarisk is unlikely, and the extent to which scattered native riparian vegetation within tamarisk stands might enhance stopover-habitat quality for avian migrants is an intriguing topic for future study (see van Riper et al. 2008).

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